BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. APRIL 18, 1963 NUMBER 184

BEHAVIOR AS A TAXONOMIC CLUE: RELATIONSHIPS OF *LISSONYCTERIS* (CHIROPTERA)

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Re-examination of the generic status and relationships of *Rousettus, sensu stricto,* and *Lissonycteris*, a supposed subgenus of *Rousettus*, has been prompted by the great differences observed between live specimens of the two genera. In 1955 and 1956, Novick was able to make extensive observations of living bats not only of these two genera but of six other pteropids as well (Novick, 1958). Of these, according to Andersen (1912), *Eidolon helvum* and *Pteropus g. giganteus* as well as *Rousettus* belong in the *Rousettus* section of the Pteropinae, *Cynopterus brachyotis luzoniensis*, *Cynopterus sphinx ceylonensis*, and *Ptenochirus jagorii* belong in the *Cynopterus* section of the Pteropinae, while *Eonycteris spelaea glandifera*, *Eonycteris robusta*, and *Macroglossus l. lagochilus* are in the subfamily Macroglossinae.

BEHAVIORAL COMPARISONS

A single wild colony of about twenty *Lissonycteris angolensis* was observed in the Belgian Congo and various wild colonies of *Rousettus amplexicaudatus*, *R. seminudus*, and *R. aegyptiacus* were observed in the Philippines, Ceylon, and the Belgian Congo, respectively. Two *Lissonycteris angolensis* were captured and one, a mature female, lived in captivity for fifteen months. Many *R. aegyptiacus* were also taken alive and observed for a period of some weeks in the Belgian Congo. One, a mature male, was kept for over nine months concurrently with the *Lissonycteris* mentioned above. In addition, some six *R. seminudus* and a dozen *R. amplexicaudatus* were observed in captivity for periods of six weeks to more than three months.

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From the very first, the differences in behavior of *Lissonycteris* and *Rousettus* were grossly apparent. These can best be described as differences in limb use and in orientation.

Limb Use

Rousettus ordinarily occupy dimly lighted caves with large entrances and sheltered retreats. Here they commonly hang in large clusters along the walls or ceiling. On the wall, they hang by their hind feet with their legs so turned that their backs are to the wall, their wings folded at their sides. They take flight by swinging their body up and rotating around their feet which remain temporarily in position here though the legs are now crossed. This position is well illustrated by Kulzer (1958), in an excellent paper on the biology of *Rousettus*. *Rousettus* also roost in crevices. Here one cannot see their undisturbed resting position but they must use all four limbs in entering and leaving such crevices. *Rousettus* can fold their wings considerably and walk awkwardly on their wrists and hind feet or they can climb vertically, head first, or move along the irregular surface of a cave or crevice ceiling using the claws of their thumbs and hind feet. When *Rousettus* roost in trees, as they do when disturbed in their caves or at night when feeding, they almost always hang by both hind feet plus one or both thumbs in a sloth-like position, one foot and one thumb on each side of the branch and their wings folded. They frequently move along the underside of the branch in this position using all four limbs. Thus, wild *Rousettus* use their wrists for walking and their thumbs for climbing, roosting, and moving along the underside of branches or fruits.

Captive *Rousettus* would roost in all of the positions described above. When they were exposed to light, they would frequently crawl into a corner of the cage floor or into their feeding dish where they would press themselves as closely as possible against their surroundings, avoiding the light on their eyes. Crawling is a not uncommon mode of locomotion for *Rousettus*, whether restricted to a cage or allowed to move freely about a room. While feeding, for example, they would crawl between the hands of a stem of bananas. In addition, they occasionally used their wrists and thumbs as pushers to readjust morsels of fruit in their mouths and *R. aegyptiacus* once was seen using the claws of one hind foot to manipulate the food in its mouth.

Lissonycteris never use their wings for locomotion other than flight. In the wild, and in captivity in a large flight room, *Lissonycteris* always roosted hanging free from the ceiling or a branch or, occasionally, hanging from an irregularity of the wall, their ventral surface out as with *Rousettus*, but never using their wrists or thumbs for support and never entering a crevice. *Lissonycteris* would hang from a branch or the ceiling by the claws of one or both hind feet. If they used both feet, characteristically both would be on the same side of the branch or irregularity. *Lissonycteris* seemed incapable of folding their wings tightly as *Rousettus* do; when roosting they hold their wings only slightly folded enveloping their ventral surface (see Fig. 5).

Lissonycteris were incapable of walking or climbing since both activities require that the wrists or thumbs be used. They moved along their roost only by releasing their hold with one foot, moving this foot along to a new hold and then following with the other foot. Such movements, always slow and inefficient, were suitable only for slightly changing their roosting position. *Lissonycteris* never landed on a horizontal surface by choice and, when forced to do so to take its fruit from a dish, its movements were awkward and incompetent. After picking up a piece of fruit, it would flap off without crawling.

Lissonycteris regularly use their hind feet, but rarely their wrists or thumbs, for handling their food. When one was handed a piece of banana, it would grasp this with its teeth. Then, having readjusted its roosting foothold, it would bring one foot down (either one with apparently equal facility) to its mouth and hold the piece of fruit with its widely spread toes while biting or breaking off a manageable fragment (see Fig. 1). Then, while chewing this fragment, it would hold the bulk of the piece of fruit, with its toes, against its chest or abdomen, frequently partly or completely covered by its wings (see Fig. 4). Rarely, when through carelessness or fragmentation it was about to drop the piece of fruit which it was chewing, the bat would regain its tooth-hold by using its wrists and thumbs as awkward pushers. Thus *Rousettus, sensu stricto*, differs from *Lissonycteris* in its use of wrists, thumbs, and hind feet in roosting, climbing, moving along branches, walking, and handling its food.

Among the other pteropids, *Eidolon* and *Pteropus*, though they never enter caves, roost in trees in much the same posture as *Rousettus*, holding on with both hind feet as well as with one or both thumbs. *Eonycteris*, in caves and in captivity, roost and move in all ways like *Rousettus*. In all of these genera the wings can be considerably folded; some also commonly roost with their wings enveloping their ventral surface. Neither *Eidolon* nor *Pteropus* can walk well on horizontal surfaces and both would probably be incapable of entering cave crevices as do *Rousettus* and *Eonycteris*. *Pteropus*, at least, use their wrists and thumbs skillfully to handle fruit and to orient the morsels in their mouth.

Cynopterus, *Ptenochirus* and, to a certain extent, *Macroglossus* also use their limbs very much as does *Lissonycteris*. All three hang from above, by their hind feet only, though, unlike *Lissonycteris*, they appear to use their thumbs for climbing up walls or along branches. The wings of *Cynopterus* and *Macroglossus* do not seem to fold in life any more tightly than those of *Lissonycteris*. Judging from pictures of *Epomophorus* (Allen, Lang, and Chapin, 1917, pl. 46) and the position of *Myonycteris*' wings in alcoholic specimens, their posture in life is also like that of *Lissonycteris*.

Lissonycteris (as also *Cynopterus* and *Ptenochirus*) tended to hold large amounts of food in their cheeks and to carry food to their roost, there to chew very slowly. When required to fly while eating, they would sometimes drop a really large piece. If *Lissonycteris* was holding a piece of fruit with its hind foot, it would either transfer this to its mouth for flight or drop it. *Rousettus* never seemed to store fruit in its cheeks or to fly with any in its mouth but, like *Eonycteris*, *Eidolon*, and *Pteropus*, generally stayed at the food source, biting and worrying off fragments and chewing these at once.

Lissonycteris would chew and crush fruit, such as melon and pineapple, until all of the juice had been expressed and swallowed and then push the remaining small bolus of fiber out of its mouth with its tongue. Banana, being non-fibrous, was swallowed completely after chewing. *Rousettus* usually ate banana and, like *Lissonycteris*, swallowed the whole fruit but when *Rousettus* ate mango, papaya, or melon, unlike *Lissonycteris*, they seemed to swallow the whole substance.

Orientation

Lissonycteris and *Rousettus* differ strikingly in their orientation. *Lissonycteris* orient entirely by vision (Novick, 1958). The captive bat was helpless in the dark and refused to fly in the dark or when blindfolded. When it was forced to fly without vision, by being thrown into the air, it always crashed into the first obstacle it met.

Rousettus amplexicaudatus, *R. seminudus*, and *R. aegyptiacus* all orient visually and acoustically (Möhres and Kulzer, 1956; Kulzer, 1956, 1958; Novick, 1958; Griffin, Novick, and Kornfield, 1958). The single *R. aegyptiacus* observed for over nine months in captivity oriented largely visually in strong light but oriented acoustically in the dark, in dim light, when avoiding intricate obstacles, and when landing or taking off. Such acoustic orientation obviously demands specializations for sound production, emission, reception, and interpretation. The brain, in particular, must be highly specialized for handling acoustic information.

In the pteropids, acoustic orientation has so far been found only in *Rousettus*, *sensu stricto*, and not in *Eidolon*, *Pteropus*, *Cynopterus*, *Ptenochirus*, *Eonycteris*, *Macroglossus*, or *Lissonycteris* (Novick, 1958). The orientation of *Stenonycteris*, a subgenus of *Rousettus*, has not been observed. The distinctness of *Rousettus*, not only from *Lissonycteris* but from a fair sample of other pteropids as well, is clearly established by its acoustic orientation and the behavioral, physiological, and anatomical features associated with it.

Summary

To summarize, *Lissonycteris* differ from *Rousettus*, *sensu stricto*, in their roosting posture, in their non-flight locomotion, and in their inability to orient acoustically. Comparing the roosting and locomotory behavior of those bats observed alive, we find that *Rousettus* resembles *Eidolon*, *Pteropus*, and *Eonycteris*, while *Lissonycteris* resembles *Cynopterus* most closely. Brief observation of live epomophorine bats and examination of pictures and preserved specimens of epomophorine bats and of *Myonycteris* suggest that in behavior *Lissonycteris* resembles these bats as well.

MORPHOLOGICAL COMPARISONS

The behavioral differences between the live bats are reinforced by less spectacular, but equally definite, characters of the more conventional taxonomic sort. These make it clear that *Lissonycteris* is far closer to *Myonycteris*, a supposed intermediate genus between the rousettine and cynopterine groups, than to *Rousettus*. They also show that *Lissonycteris* and *Myonycteris* form a natural group probably intermediate between the rousettine and epomophorine groups, and one whose resemblances to the cynopterines are more apparent than real.

The rousettine and cynopterine sections of the Pteropinae are chiefly distinguished by the following characters possessed by the latter and not by the former: The rostrum is shortened and the facial axis is not deflected, M_3 and usually M^2 are lost, the eyes are larger, and there is a tendency to form tubular nostrils. The differences in the ridges of the soft palate described by Andersen (1912, pp. lx, 485, 591, figs. 29A, 50) are also characteristic.

On the basis, largely, of these characters, Andersen points out that *Myonycteris* is somewhat intermediate between the cynopterine and rousettine sections. He says (1912, pp. lvi-lvii): "*Myonycteris* . . . has in many respects remained on the Rousettine level of development, while in others it exhibits modifications approaching those of *Cynopterus*. The general appearance, the dental formula, and the palate ridges are quite or nearly as in *Rousettus*, but the rostrum is conspicuously shortened, the facial axis less deflected, m_3 and m^2 (last lower and upper molar) reduced almost to rudiments, the orbits larger, the nostrils more prominent and the calcar weaker," and later (p. lxi): "The fact is that this genus has retained many characters of *Rousettus*, while in practically all the features in which it differs from *Rousettus* it more or less closely approaches to *Cynopterus*. Whether a genus exhibiting characters of this description ought, in a linear arrangement, to be classed at or near the end of the Rousettine section or as the 'opening' genus of the Cynopterine section, must necessarily remain a matter of opinion."

The resemblance of *Lissonycteris* to *Myonycteris* in all the above traits, except the shortening of the rostrum and reduction of the dentition, was not noted by Andersen when he classified the former as an aberrant form related to but possibly generically distinct from *Rousettus* (*op. cit.*, 1912, p. 814). At the same time he does note (1912, p. xlix): "the brain case [*Lissonycteris*] is peculiarly flattened posteriorly and the facial axis even less deflected than in *Rousettus*, both characters giving the skull, viewed in profile, a rather striking resemblance to *Epomops*."

EXTERNAL CHARACTERS

Actually, in addition to the rather generalized myonycterine characters given above, both *Lissonycteris* and *Myonycteris* have a number of traits in common which the small size of *Myonycteris* and the superficial resemblance of *Lissonycteris* to *Rousettus* have tended to mask. Chief among these, externally, is the development of the wing in these two genera which greatly exceeds that of *Rousettus*. Though it is more similar in size to that in *Cynopterus*, it is different in proportions. The size difference shows most conspicuously in the greater length of the combined metacarpal and first phalanx of digits three to five as compared with length of forearm. The following comparison of finger lengths refers only to these two joints. In *Lissonycteris*, the fifth finger is conspicuously longer than the forearm; in *Myonycteris*, the slightly smaller wing has digit five subequal in length to the forearm. In *Rousettus*, the fingers are much shorter; usually only digit three has the upper joints as long as the forearm; occasionally three is somewhat longer and four is subequal to the forearm. In all three genera, these two joints of digit five are shortest though the relative lengths vary specifically. *Cynopterus*, while longer fingered than *Rousettus*, is less extreme than the other two genera and differently proportioned. The metacarpal and first phalanx of digits four and five are subequal in length, with four being slightly shorter than five which is about the same length as the forearm, while digit three is conspicuously longer.

Other differences in ratios of wing bones can be worked out, but the most significant fact is that in development of the wing *Lissonycteris* and *Myonycteris* are not intermediate between *Rousettus* and *Cynopterus* but differ equally from both. The same is true of the attachment of the wing which in the two former genera is near the middle of the first phalanx of the second toe, in *Cynopterus* is near the distal end of the first phalanx of the first toe, and in *Rousettus* is usually between metatarsals one and two, sometimes near the bases of the first phalanges, often well proximal to this.

Lissonycteris and *Myonycteris* are also equally distinct from the other two genera in shape and arrangement of the odontoid papillae. These papillae, which border the lips, inside, from the angle of the mouth forward, are rather high and pointed and, in *Lissonycteris*, form a single row extending about to the canines. In *Myonycteris*, the shape and arrangement of the papillae are about the same, but in some instances on the upper lip toward the angle of the mouth there is a poorly defined second row. In *Rousettus*, the single row of small papillae is much reduced in extent and size. In *Cynopterus*, the more numerous, larger papillae are irregularly arranged in a broad band two or three rows wide and somewhat better developed on the upper than the lower lip.

The arrangement of the palatal ridges in *Lissonycteris* is very different from that in *Cynopterus* and, while more like that in *Rousettus*, differs in certain details which again point up *Lissonycteris*' close resemblance to *Myonycteris*. In the two latter, the three anteriormost ridges are not divided and scarcely, if at all, bowed forward; four and five are divided in the middle, slope forward (as in *Rousettus*), and have the inner ends recurved; six and seven, which lie behind the tooth row, are similarly shaped and these last four converge somewhat at their medial ends. Behind this, there are two or three other poorly defined ridges. *Rousettus* differs in general in having the anterior ridges more bowed forward, number four usually not divided, and the posterior ridges more nearly parallel with each other.

Other external characters which set *Lissonycteris* and *Myonycteris* apart from *Rousettus* are the shorter, less robust tail, the longer, denser fur on the notopatagium and on the proximal, dorsal surface of the tibia, the smaller foot with the basal quarter to third of the first phalanges webbed (see Fig. 1), the more slender claws, the more delicate calcar, and the extensive patch of glandular fur on the throat of adult males.

HAIR STRUCTURE

Additional evidence of the close relationship of *Lissonycteris* and *Myonycteris* comes from Benedict (1957) who says that they have essentially the same hair structure: the pigment distribution, absence of a medulla, and form, arrangement and dimensions of the scales being alike. The slight difference she describes in the more distal maximum diameter of the hair in *Myonycteris* seems scarcely important. The hairs of *Cynopterus* are so different as not to need comparison here. Those of *Rousettus* are less compellingly so, being similar in pigment distribution and absence of a medulla. They apparently differ however in arrangement and size of scales and, to a certain extent in their form. In general, these differences seem more of degree than kind.

CRANIAL CHARACTERS

Cranially, as externally, *Lissonycteris* and *Myonycteris* possess a number of features in common which distinguish them equally from *Rousettus* and *Cynopterus*. In addition to the proportions of the skull as a whole, the shape and spacing of the teeth, the occlusion pattern, and the structure of the interorbital region are particularly important. In general proportions, the dominant feature of the small *Myonycteris* skull, and one in which it agrees with the much larger *Lissonycteris*, is the relatively great length of the anterior part of the skull (measured from behind the postorbital processes to the tips of the premaxillaries) as compared with both length of the brain case (measured from behind the postorbital processes) and its bulk. Typically, also, the brain case in *Myonycteris* is elongated behind the temporal root of the zygomatic arch, and the rostrum is slender with the posterior ends of the nasals depressed giving the skull in profile a dish-faced appearance, an appearance that is accentuated by the great development of the lateral of the two pairs of frontal sinuses.

Compared with *Rousettus*, *Lissonycteris* and *Myonycteris* have a more slender rostrum. In the two latter, a projection of a line along the top of the nasals passes ventral to the top of the orbit and the brain case. In *Rousettus, sensu stricto*, such a line passes dorsal to both of these points. In the myonycterines, the brain case is elongated and flattened so that the distance from the bottom of the occipital condyles to the top of the occipital crest is less than the distance from the postglenoid process to the back of the condyle, whereas in *Rousettus* the first distance is equal to or greater than the second. The larger orbit, though difficult to measure, is easy to see. In *Lissonycteris* and *Myonycteris* the diameter of the orbit taken approximately parallel to its antero-rostral margin is equal to or greater than the lacrymal width; in *Rousettus* it is less. Further, the antero-ventral border of the orbit formed by the root of the zygomatic arch is a better developed, sharper edged rim; it is thin and plate-like where the infraorbital canal pierces it. The thicker root in *Rousettus* results in a noticeably longer canal.

When *Lissonycteris* and *Myonycteris* are compared with *Cynopterus,* the angle of the nasals, the elongation of the back of the skull, and the rather large orbit with a short infraorbital canal show no striking differences. That these similarities are indicative more of parallelism than relationship is suggested by the pronounced differences in overall proportions of the skull. The short, heavy rostrum and relatively large brain case of *Cynopterus* contrast sharply with the more slender nosed, less chunky skulls of *Lissonycteris* and *Myonycteris.* Such features are hard to measure, but in *Cynopterus* the distance from the postorbital foramen to the back of the occiput is much longer than the distance from this foramen to the premaxillary suture, while in *Lissonycteris* and *Myonycteris* these distances are almost equal; further, the height of the brain case vertically above the interpterygoid region is usually a third or more of the length of the skull in the former, while in the two latter it is usually considerably less than one-third of this length.

Certain features of the frontal sinuses are also very distinctive. Characteristically, those of *Lissonycteris* and *Myonycteris* have the lateral pair much more inflated than the medial. This, together with the tilting up of the orbital margin posteriorly, makes the interorbital region concave. In *Rousettus,* the reverse is true; the smaller, lateral pair of sinuses are relatively less inflated, the medial more, and the orbital margins are not tilted up, so the interorbital region is flattened or domed, sometimes with a median sulcus anteriorly. In all three of these genera, the lateral pair of sinuses end in front of the postorbital foramina. In *Cynopterus,* on the other hand, the well inflated lateral pair extend at least to the level of the postorbital foramina which are thus crowded outwards into the postorbital processes, and the much smaller, medial pair show scarcely any inflation.

DENTITION

In past classifications, the reduction of the last molars has been one of the most important reasons for grouping *Myonycteris* with *Cynopterus,* while the number of teeth has been used to relate the former to *Rousettus.* Actually, the shape of the anterior teeth is far more important than either of these in showing generic relationships and is one of the most clearcut characters relating *Lissonycteris* and *Myonycteris.* Variation at the end of the molar row is, on the other hand, an important differential character separating these latter two. Typically, the cynopterine bats have lost the last upper and lower molars, while these teeth are retained and well developed in the rousettine group. Both *Lissonycteris* and *Myonycteris* have the rousettine formula but, in the latter, the last molars are tiny and clearly obsolescent, while in the former they are the opposite. Reduction of the molars in *Myonycteris* is no more reason than their stronger development in *Lissonycteris* for grouping the one with *Cynopterus* and the other with *Rousettus*.

The structure of the teeth, their spacing, and the occlusion pattern are remarkably similar in *Myonycteris* and *Lissonycteris* and differ equally from both *Cynopterus* and *Rousettus*. The most striking feature of the tooth rows of *Lissonycteris* and *Myonycteris* is the wide spacing of the short, broad teeth; in addition, the anterior teeth have the main external cusps placed well back on the outer margin so that in profile the teeth look more equilaterally triangular. The teeth in *Cynopterus* differ sharply in being larger and more crowded, and in the arrangement of the cusps, with the main external cusp more anterior and a deeper sulcus separating the inner and outer halves of the teeth. In the upper jaw of *Cynopterus*, P^3 has a well marked ridge or internal cusp, whereas in *Lissonycteris* and *Myonycteris* this tooth, though thick, is simple. In the lower jaw of *Cynopterus*, P_1 is relatively large and P_3 compared to P_4 is conspicuously higher, almost as broad, but shorter with a less well developed heel. In *Lissonycteris* and *Myonycteris* P_1 is tiny and P_3 reduced, much narrower and only slightly higher than P_4, with no trace of a heel; P_4 is relatively large with a high, almost central, main cusp, bilobed in *Lissonycteris* and in *Myonycteris* with sometimes a suggestion of a heel. In general, these premolars are more similar to those of *Rousettus;* in the latter, P^3, P_3, and P_4 are simple, high, and differ from *Lissonycteris* and *Myonycteris* chiefly in having the single cusp set farther forward with a trace of a heel posteriorly. P^4 has the more usual pteropid elongated shape with the main cusps forward and the inner margin sometimes bilobed. In the lower jaw, neither of the first two premolars of *Rousettus* is reduced, as in the former genera, while the molars are longer and narrower.

The wide spacing and simple shape of the teeth in *Lissonycteris* and *Myonycteris* relate to a very characteristic occlusion pattern in which the P_3 and P^3 alternate with each other, P_4 barely occludes with the posterior edge of P^3, and there is scarcely any more contact between P^4 and the posterior edge of P_4. In *Rousettus,* the overlapping of the teeth is more pronounced, correlated with the beginning of a heel. In *Cynopterus*, it is even more so with the crowded teeth slanting forwards and P_3 reaching the back of the upper canine.

On the basis of the material at hand, *Myonycteris* and *Lissonycteris* differ sufficiently from each other to warrant generic distinction. However, it may be significant that *M.* (*Phygetis*) is distinguished from *M.* (*Myonycteris*) by its relatively larger teeth, especially M^2 and M_3, and the bilobed main cusp of P_4, characters which also help distinguish *Lissonycteris* from *Myonycteris, sensu stricto*. Further, two small species of *Lissonycteris*, *smithii* and *crypticola*, which are described as having reduced dentition, may prove to be somewhat intermediate between the two genera. Study of these possibly annectant forms may make it necessary to reconsider the generic status of *Lissonycteris*. For the present it seems best to retain both as full genera.

DISCUSSION

While the results of this study point up the distinctness of the myonycterine from both the cynopterine and the rousettine sections of the Pteropinae, they also suggest that the former may be more closely related to the epomophorine section than has previously been supposed. A casual inspection of the epomophorines and myonycterines shows such extreme external differences, such differences in structure of the palate, posterior bony nares, shape of the molars and tooth formula, and such a greatly elongated rostrum in many epomophorines that any close relationship might seem most unlikely. However, in the rather unspecialized genus *Epomops*, the little or not deflected skull, the relative size as well as shape of the brain case and rostrum, the details of the interorbital region, and the size of the orbits all show a strong resemblance to *Lissonycteris*. In similar ways, *Epomophorus labiatus*, except for its elongated rostrum, resembles *Myonycteris*. There are other resemblances. In the epomophorines, the wide spacing of the teeth and the consequent alternating more than overlapping occlusion pattern of the anterior ones as well as the more posterior position of the main cusps of both upper and lower third and fourth premolars and the small size of the first lower premolar all suggest the myonycterine group. The characteristic tooth formula of the epomophorines is foreshadowed by the great reduction in *Myonycteris* of those teeth which are lacking in the former. Externally, the long-fingered wing, in which the metacarpal and first phalanx of digit five is a little longer than the forearm in *Epomops*, and the attachment of the wing membrane in this and most of the epomophorine bats to the first phalanx of the second toe are also characteristically myonycterine. Finally, though the arrangement of the palatal ridges is highly variable from species to species, in one form at least of *Epomops* the divided fourth and undivided, straight first three ridges are not unlike those in *Lissonycteris*.

The epomophorine affinities of *Lissonycteris* and *Myonycteris* are further indicated by Benedict (1957, p. 292): "Strikingly, the scale form of *R. angolensis* [*Lissonycteris angolensis*] is more similar to that of the *Epomophorus* section than to the *Rousettus* section to which Andersen assigns it." and "The scales of *Myonycteris* are virtually indistinguishable from those of the *Epomophorus* section."

Analyzing the differences between the epomophorines and myonycterines, we find that the most conspicuous ones usually are found in the regions of the skull where, within the epomophorine group, there is much generic variation, or that these differences are more extreme developments of traits which *Lissonycteris* and *Myonycteris* already show. This suggests that the epomophorine is a specialized branch of the myonycterine group which in turn is fairly close to an early *Rousettus*-like stock. These annectant forms, the myonycterines, help to confirm Andersen's (1912, liii-lvi) supposition that the origin of the epomophorine group was from a primitive and *Rousettus*-like stock.

The cynopterine bats are clearly quite different. Resemblances between these and *Myonycteris* such as tooth formula, shortening of the rostrum, slight elongation of the back of the skull, reduction of the tail, and development of the wing as well as roosting and locomotory behavior are probably parallel developments in groups which diverged early. Andersen also supposes that the cynopterine bats arose from early *Rousettus*-like ancestors, but, with *Myonycteris* eliminated as an intermediate form, the two groups are more sharply distinct than was previously supposed.

Geographically, the picture presented by the morphological evidence is a very logical one. The cynopterine bats become exclusively an Oriental and Austro-Malayan group, the epomophorines are restricted to Africa where they center in the western forested regions, and in this same general area we find the rather more primitive but fairly closely related myonycterine group. Common to both regions is the rousettine group considered, on the basis of morphological characters, to be the most primitive and therefore probably the most direct descendant of the ancestral stock from which all arose. The occurrence of a highly developed sonar system in the otherwise not particularly specialized *Rousettus* suggests, however, that they are farther removed from the ancestral stock than was previously supposed.

ACKNOWLEDGMENTS

This work was supported in part by the Office of Naval Research[1], the United States Public Health Service, the Sigma Xi-RESA Fund, the Belgian American Educational Foundation, and Harvard University. During part of this period, Novick was a Fellow of the National Institute of Neurological Diseases and Blindness. For help in capturing and keeping these bats, we are grateful to the personnel of the Sangley Point Naval Air Station and Clark Air Base in the Philippines, to the Naval Attachés and other personnel of the American Embassies in the Philippines and Ceylon, to Mr. Pablo Tanciojo and the Negritos of the Zambales Mountains of Luzon, to Capt. J. A. Simon, USAF, to Major A. Weinman of the Dehiwela Zoo, Ceylon, and to Mr. and Mrs. W. W. A. Phillips formerly of Namunukula, Ceylon, to Dr. Louis van den Berghe, Messrs. J. Moureau, P. Pirlot, and G. Marlier of the *Institut pour la Recherche Scientifique en Afrique Centrale*, Lwiro, Belgian Congo, and to countless others who made these studies possible by giving of their time or experience. We are most deeply indebted to Dr. D. R. Griffin of Harvard University for help of every description.

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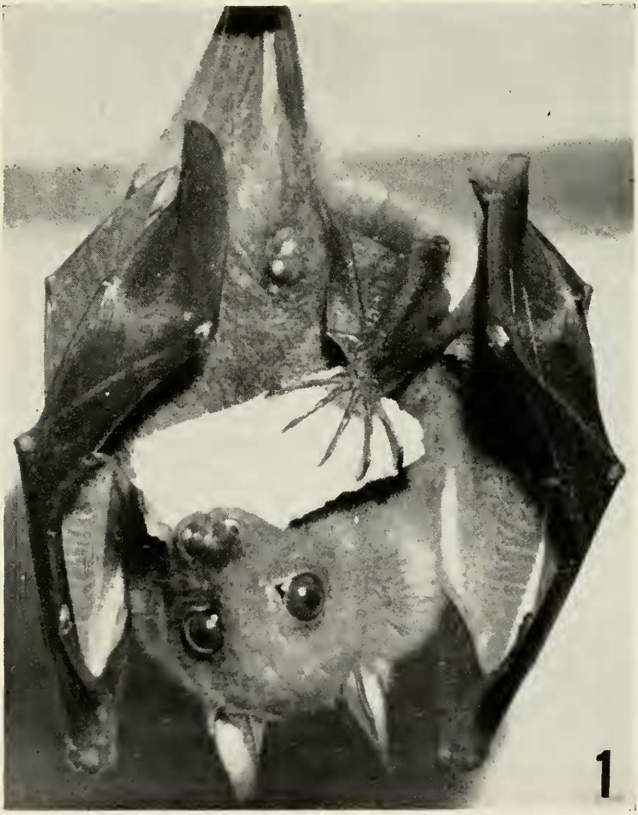
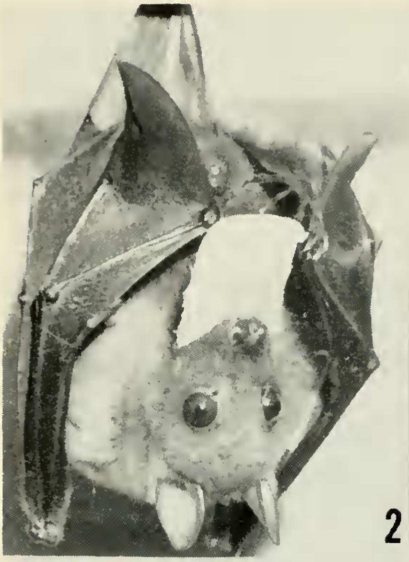


Figure 1. *Lissonycteris angolensis* hanging from slat by the left foot (not visible), holding a piece of banana with its right foot, while biting off a manageable portion.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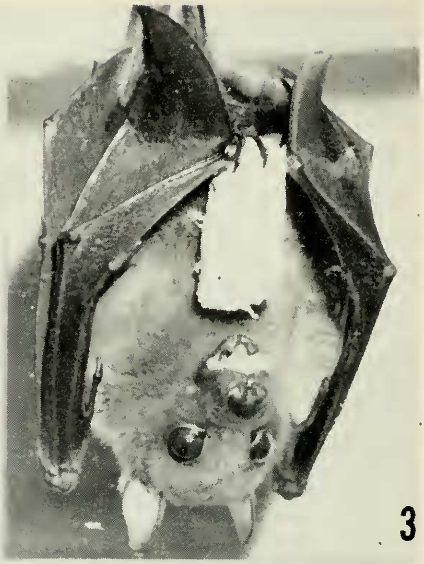
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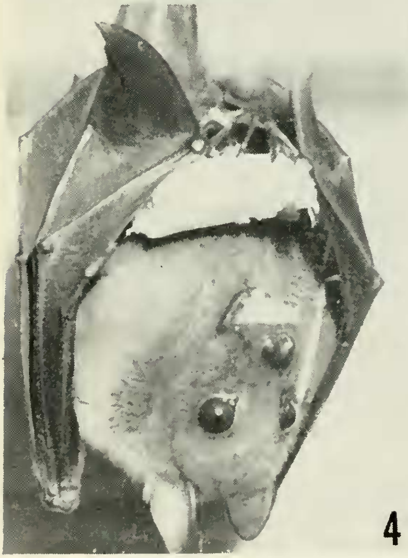
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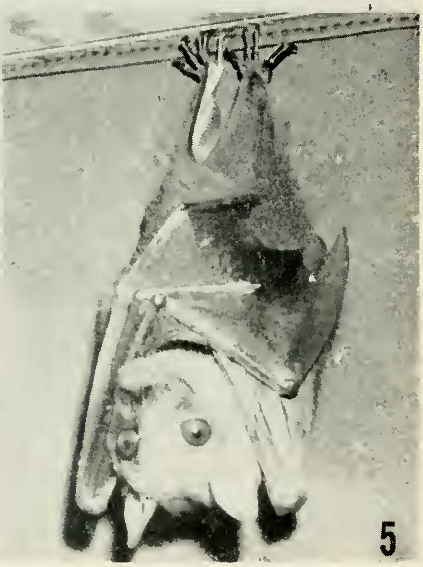
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Figures 2, 3, and 4. *Lissonycteris angolensis* handling pieces of banana. The use of the foot in handling food and the posture of the wings while doing so is clearly shown.

Figure 5. *Lissonycteris angolensis* resting, hanging on a canvas wall at its junction with the ceiling. Note the position of the feet which can hold onto a roost equally well in this or the opposite orientation. The wings are being held well overlapped, substantially enwrapping the body. If the bat had not been disturbed by the photographer, its chin would have been tucked against its chest and its eyes closed.